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## The Tribe Osirini, its Scope, Classification, and Revisions of the Genera *Parepeolus* and *Osirinus* (Hymenoptera, Apoidea, Anthophoridae)<sup>1</sup>

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### ABSTRACT

The limits of the hitherto monotypic tribe Osirini are expanded to include *Epeoloides*, *Parepeolus* and three new genera: *Ecclitodes*, *Osirinus* and *Protosiris*. It is suggested that the tribe does not belong in the subfamily Nomadinae, but represents a group of parasites independently derived from pollen-collecting ancestors. A cladistic analysis, a key and descriptions are presented for the genera. For *Parepeolus* and *Osirinus* keys to the species, synonymies and descriptions are provided; four new species are described.

### INTRODUCTION

The present paper has three objectives. First, to argue that the monotypic tribes Osirini and Epeoloidini, the hitherto unplaced genus *Parepeolus* Ducke and the new genera *Ecclitodes*, *Osirinus* and *Protosiris* constitute a monophyletic group, the Osirini. Second, to suggest that the tribe so constituted does not belong in the subfamily Nomadinae, but is better understood as an independently derived group of parasitic bees within the Anthophorinae. Third, to

present an analysis of the relations among the genera of Osirini and revisions of certain genera.

This study was triggered by the discovery of some bees, particularly the new species *Osirinus lemniscatus*, that were obviously related to *Osiris* Smith by characters of wing venation and genitalia but had a very different aspect. The build of the body resembled that of *Parepeolus* and *Ecclitodes*. Indeed, at first sight *O. lemniscatus* looks much like the

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Chilean *E. stuardi* (Ruiz). Some of those bees have dark integument but others are definitely pale. Such annectant forms, several previously described as *Osiris*, are grouped here in two new genera. The Holarctic genus *Epeoloides* Giraud should also be included in the group. Warncke (1982) has already suggested a close relation of *Epeoloides* to the South American *Parepeolus*, based on overall similarity.

Previous treatments of the group are restricted to *Osiris* and *Epeoloides*, and *Parepeolus* has seldom been mentioned in the literature since its description by Ducke (1912). Important accounts of *Osiris* are those by Friese (1930), Grütte (1935), Popov (1939), Michener (1944, 1954) and the recent generic revision by Shanks (1986). Important accounts of *Epeoloides* are those by Linsley and Michener (1939) and Popov (1958). Both genera have long been considered as isolated elements, each forming a tribe. The tribal name for all the groups mentioned above should be *Osirini* according to Michener (1986).

The *Osirini* occur in the Holarctic and

Neotropical regions. *Epeoloides* (3 species) is found in the eastern half of North America and in Europe, with the easternmost record at 58° East longitude in the Soviet Union. *Osiris* (over 20 species) ranges from Mexico to northern Argentina. *Parepeolus* (4 species) and *Osirinus* (3 species) range from northern Brazil to central Argentina. *Protosiris* (4 species) occurs from Panama to southern Brazil and Bolivia, and *Ecclitodes* (2 species) is restricted to Chile and southern Argentina. The two genera showing the most plesiomorphies, *Epeoloides* and *Ecclitodes*, occur at the extremes of the distribution.

Most arguments presented below for excluding the *Osirini* from the *Nomadinae* also hold for *Coelioxoides*, a genus that has been considered many times as a relative of *Osiris* due to the peculiar modification of the sixth sternum of the female. *Coelioxoides* does not possess the apomorphies of *Osirini*, and the shape of the sternum is clearly convergent, as indicated by the terminal position of *Osiris* in the cladogram. The relations of *Coelioxoides* will be treated elsewhere.

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#### MATERIAL AND METHODS

Material studied, including types, was obtained from several collections. I am indebted to the following: American Museum of Natural History, New York, J.G. Rozen, Jr. (AMNH); R.B. Brooks, Lawrence, Kansas; Cornell University, Ithaca, G.C. Eickwort and B. Alexander; Florida State Collection of Arthropods, Gainesville, L.A. Stange (FSCA); M. Fritz, Rosario de Lerma, Salta; Instituto Miguel Lillo, Tucumán, A. Willink; Los Angeles County Museum, Los Angeles, R.R. Snelling; Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo de La Plata, La Plata, R. Ronderos (MLP); R.B. Roberts collection, Rutgers University, New Brunswick (RBR); Snow

Entomological Museum, University of Kansas, Lawrence, C.D. Michener (SEM); Universidade Federal do Paraná, Curitiba, J.S. Moure (UFPR); Zoologisches Museum, Humboldt-Universität, Berlin, F. Koch. The acronyms are used below to indicate depositories of specimens.

Morphological terminology of Michener (1944, 1965) has been followed, except that metapostnotum is used instead of propodeal triangle (Brothers, 1976). In the descriptions the metasomal terga (T) and sterna (S) are identified with Arabic numerals. For easy comparison characters are numbered in the generic descriptions. Diagnostic characters are italicized.

## RELATIONSHIPS OF THE OSIRINI

The monophyly of the tribe Osirini is supported by two synapomorphies: the ventral sclerite in the cervical membrane and the carina along the inner and basal ventral margins of the forecoxa. The presence of a ventral sclerite in the cervical membrane is unique among bees. It is independent and united by membrane to the postgenal bridge that closes the foramen magnum ventrally (fig. 4). In other bees there may be a faint sclerotization of the membrane (as in many long-tongued bees). The ventral cervical sclerite is round, usually with a posterior carina. A similar sclerite is present in sphecoid wasps of the subfamily Philanthinae. The forecoxal ventral carina is always complete along the inner margin, but the basal sector varies in extent. A similar carina is found in the subgenera *Heterocentris* and *Hemisiella* of *Centris* (Snelling, 1984), obviously independently derived. The tribe Osirini may be further characterized by the epistomal suture faded laterally so that there is no separation between clypeus and paracocular area near the eye, by the vestiture of the thorax usually consisting of long, plumose hairs, and by the presence of an extruded, upcurved sting visible in some pinned specimens. The last character is seen only sporadically; I have observed it in specimens of *Parpeolus*, *Ecclitodes* and *Osiris*, but not in *Epeoloides*, *Osirinus* or *Protosiris*. I have failed to find a satisfactory explanation for such exerted stings. The sting is impressive in *Osiris* (Friese, 1930, fig. 3; Shanks, 1986, fig. 42), but in other genera it is not much different from that of pollen-collecting bees, except for the proportionally longer rami and furcula. Many nomadines (e.g., Epeolini) also have stout stings with long rami and furculae, but they are never so extruded. The depressed metasoma of most osirines may be the concurrent factor that leads to such upcurved stings; in this case *Epeoloides*, with a moderately depressed metasoma, is not expected to have an upcurved sting.

The genera of Osirini have been placed previously in the Nomadinae. The apomorphies that best indicate the monophyly of the subfamily Nomadinae are those presented by Rozen (1966) and Rozen et al. (1978) based on morphology of the larvae and adult behavior (oviposition pattern). Those characters, however, are not known for the Os-

irini. There are some characters of adult morphology unique for the Nomadinae and useful in defining the group, even though exceptions occur in one or more tribes for each character. These are: 1) Retraction and concealment of the sixth metasomal sternum of the female (partial in Protepeolini). 2) Sixth metasomal sternum of the female apically emarginate, ending in two points (exceptions are Protepeolini, Isepeolini and *Nomada*). 3) Sixth metasomal sternum of the female bearing spine-like setae (exceptions are Protepeolini, Neolarrini, Ammobatini and Caenoprosopidini; variable within Isepeolini). 4) Fifth metasomal tergum of the female with a specialized apical area of hairs, the pseudopygidial area (exceptions are Towsendiellini, Neolarrini, Ammobatini and Caenoprosopidini; a hairy apical flap in the Isepeolini is probably not homologous with the pseudopygidial area.) The tribes Isepeolini and Protepeolini are the most problematic groups in the above characterization of the Nomadinae.

Osirini do not share any of the features just mentioned. The sixth metasomal sternum of the female does not differ much from the condition seen in pollen-collecting bees (figs. 37, 39), with the exception of *Osiris*, which shows a trend in elongation of the segment different from any trend seen in the Nomadinae. A pseudopygidial area is absent. Furthermore, nomadines lack a stipital comb, or it is weak (as in *Biastes*, Winston, 1979), a feature considered characteristic of the parasitic syndrome in long-tongued bees (Michener, 1944). In Osirini, on the contrary, the stipital comb is developed and frequently occupies a concavity much as in many pollen-collecting bees.

In all the above comparisons it is possible to argue that the condition in Osirini is plesiomorphic. Hence the group could not have arisen from within the nomadines, but it may still constitute the most primitive representative of that lineage.

Further features in which Osirini differ from nomadines suggest possible connections to other anthophorid groups: 1) The Exomalopsini have along the outer surface of the stipes a sclerotized ridge (Winston, 1979); the length and position of the ridge is identical in Osirini (figs. 5, 14, 24, 30, 34, 45, 52); the ridge is absent in Nomadinae. 2) The sternal region behind the third apo-

physeal pit is produced into a triangular lamella, which in Osirini is translucent, not punctate, and arched. A similar condition is found in *Melecta*, *Emphorini* and many *Exomalopsini*. In most *Nomadinae* the triangular projection is thick (not translucent), flat and punctate (exceptions are some *Brachynomada*, *Nomada* and *Paranomada* with extensively impunctate integument and *Isepcolus* with the triangular projection thick and punctate, but arched). 3) The fifth metasomal tergum of the female in Osirini has a wide, polished apical margin bordered by long hairs. A similar condition is present in the *Melectini*. 4) The marginal cell in Osirini is separated from the wing margin for its entire length, so that there is a membranous costal rim as wide as the radial vein; the rim even continues along the pterostigma. This is not the condition in the *Nomadinae*; in the *Anthophorinae* various degrees of separation are present, the *Tetrapediini* have a well developed rim (Michener and Moure, 1957). This list does not represent an exhaustive comparison of the Osirini with the many tribes of the *Anthophorinae* (such a task is outside the

scope of the present paper) but is suggestive of possible relationships.

Since biological information indicates that at least some of the Osirini are parasites of *Exomalopsini*, and in consideration of the morphological affinities between the two tribes mentioned above, it is tempting to think of a close relationship between these two tribes. However, characters of osirine male genitalia that may be considered plesiomorphic among anthophorid bees (gonobasal ring complete, not fused ventrally to the gonocoxites, volsellae present, well developed dorsal ramus of the gonostylus) preclude the derivation of Osirini from any extant *Exomalopsini*.

From the above discussion it appears that there is no support for including the tribe Osirini in the *Nomadinae* and that they may represent a group of parasites independently derived from pollen-collecting ancestors, as do the *melectines*, *rathymines* and *ericrocines*. Regarding the position of the Osirini in the current classification, I suggest considering them as a tribe in the subfamily *Anthophorinae*, pending a comprehensive revision of the members of this subfamily.

#### GENERIC ANALYSIS OF THE OSIRINI

The cladogram in figure 1 was constructed by hand, taking as outgroups the other tribes of *Anthophorinae*, paying particular attention to those mentioned above as sharing some features with the Osirini. Since relations of Osirini are not certain, all tribes were considered to form a polytomy for outgroup comparison. Only those characters for which the polarity was clear were used in constructing the tree. Many more characters discussed below may become cladistically relevant when the relations of Osirini are better understood.

The branch that leads to *Epeoloides*, *Osirinus*, *Protosiris* and *Osiris* is supported by two genitalic characters (10, 11): the unusual curvature of the apodeme of the penis valve (figs. 26, 41, also figures in Michener, 1954, and Shanks, 1986) and the shape of the dorsal gonocoxal bridge. The common condition in anthophorids is that the dorsal basal union of the gonocoxites projects into the capsule as a prong or a plate. Such a projection is recurved and apically truncate

in the genera on the right branch of the tree (figs. 26-27, GCX, 40-41). In *Parepeolus* and *Ecclitodes*, even if smaller, it is pointed, the plesiomorphic condition.

The two main branches of the tree are further characterized phenetically. *Epeoloides*, *Osirinus*, *Protosiris* and *Osiris* share an elongate jugal lobe, lateral margin of clypeus continued upward by a carina, basal vein of forewing arising apical to vein cu-v (both veins meeting in *Osirinus fritzi* and females of *Epeoloides coecutiens*) and basal sector of forecoxal carina extended all the way across the coxa. *Parepeolus* and *Ecclitodes* have a small, round jugal lobe, no carina continuing the margin of the clypeus, basal vein arising basal to vein cu-v (both veins meeting in two species of *Parepeolus*) and basal sector of forecoxal carina short (fig. 4).

The position of *Epeoloides* in the cladogram is interesting in view of its Holarctic distribution and host relationship to the *Melittidae*; all other genera are Neotropical and probably associated with *Exomalopsini*.



and ventral views of the sixth sternum of an *Exomalopsis* (fig. 39) are illustrated for comparison. Besides the apomorphies shown in the tree, *Osiris* has the inner margin of the

eye gently emarginate in the upper third, a sharp preoccipital ridge behind the ocelli and the hypostomal carina forming a right angle when it reaches the mandibular socket.

TABLE 1. LIST OF APOMORPHOUS CHARACTERS. Outgroups are other tribes of Anthophorinae. Apomorphous characters were coded (1), or if further derived as (2).

1. Cervical membrane with ventral sclerite present (fig. 4) (1). Outgroups with sclerotization faint or absent. (The sclerite is small in *Epeoloides coccutiens* but well developed in *E. pilosula*).
2. Forecoxa with ventral carina (fig. 4) (1). Carina absent in outgroups. (A similar carina has arisen independently in two subgenera of *Centris*).
3. Apex of marginal cell pointed, close to costal wing margin (fig. 28) (1). Marginal cell sometimes pointed in outgroups, but apex bent away from wing margin. (Apex of the marginal cell close to the costal margin is the usual condition in short-tongued bees but is rare in anthophorids; it is also found in several Nomadini, to which *Osiris* was thought to be related).
4. Stipital comb-bearing concavity reduced (figs. 5, 24) (1). Stipital comb-bearing concavity present in most outgroups (except Melectini); presence of such concavity plesiomorphic for long-tongued bees in general (Winston, 1979; Michener and Greenberg, 1980).
5. Maxillary palpus with 4 or 5 segments (1). Plesiomorphic condition is 6 segments. (Species of *Parepeolus* have 4 or 5 segments.)
6. Legs elongate, scarcely hairy; hairs mostly simple (1). Legs stout, with abundant plumose hairs in pollen-collecting anthophorids. (Elongate legs with few hairs also occur in one other parasitic group, the Rhathymini. Since both states of the character occur in the Osirini, the polarity was based on the assumption that a reversal is unlikely).
7. Dorsal branch of gonostylus absent (1). Gonostylus with 2 branches plesiomorphic for anthophorid bees in general. (Most tribes of Anthophorinae, except Eucerini, have at least a few taxa with 2-branched gonostylus. Reduction of the gonostylus, or fusion to the gonocoxite in such a way that it is not distinguishable, is a common trend usually associated with overall simplification of the genitalia, and evidently derived).
8. Dorsal branch of gonostylus flattened (fig. 7) (1). Dorsal branch of gonostylus flattened and enlarged (figs. 17, 19, 21) (2). Dorsal branch not flattened and smaller than ventral branch in outgroups.
9. Ventral branch of gonostylus bifid (figs. 7, 17, 19, 21) (1). No such bifid gonostylus in outgroups.
10. Internal projection of dorsal bridge of gonocoxite truncate (figs. 7, 40, 48) (1). Internal projection of dorsal bridge pointed or lamellate in outgroup.
11. Penis valve with apodeme curved dorsally (figs. 26, 41) (1). Apodeme not so curved in outgroups.
12. Pterostigma strikingly large, more than 7 times length of prestigma (1). Pterostigma in outgroups variable, usually less than 4 times length of prestigma (exception is *Paratetrapedia* within *Exomalopsis*).
13. Mandible long, sickle shaped (figs. 44, 47) (1). Mandible in outgroups not strongly curved.
14. Mandible with 2 subapical teeth (1). Plesiomorphic condition for anthophorid bees in general is one subapical tooth (Michener and Fraser, 1978). (Presence of two subapical teeth is a rare feature among parasitic anthophorids; besides *Osiris*, it is also found in some Isepeolini).
15. Dorsolateral lobes of pronotum bulging (1). Lobes not bulging in outgroups.
16. Anterior dorsal margin of pronotum broadly recurved (1). Anterior dorsal margin of pronotum straight or slightly recurved in outgroups.
17. S6 of female elongate, distally tubular, forming a sheath for the sting (fig. 55) (1). Sternum not so in outgroups. (*Coelioxoides* has an elongate S6, independently derived).
18. T6 of female with rim apical to pygidial plate (fig. 51) (1). Unique feature of *Osiris* (Grütte, 1935).
19. Pygidial plate of male absent (1). Pygidial plate present is plesiomorphic for bees in general. (Absence of the pygidial plate occurs in some of the outgroups, but in every case it is interpreted as the derived condition).
20. Posterior lateral margin of pronotum deeply emarginate below pronotal lobe (fig. 54) (1). No such deep emargination in outgroups (probably related to character 15).
21. Metapostnotum microstriated (1). Unique feature of *Ecclitodes*, not present in outgroups.
22. Supratregular carina directed anteriorly, diverging from tegular margin (fig. 11) (1). Unique feature of *Parepeolus*, not present in outgroups.
23. Eyes of male strongly convergent above (1). Similar convergence found in a few other bees, but not in outgroups.
24. Pygidial plate of male spatulate (1). Pygidial plate with sides parallel or converging apically in outgroups.

The species excluded from *Osiris*, together with new ones described below, are recognized as belonging to two new genera. *Protosiris* shares with *Osiris* the slender habitus, long legs, sparse vestiture and elongate pterostigma. Shanks (1986) recognized the group as a species-group within *Osiris*. She characterized it by the short head, the parallel inner margins of the eyes, the mandible with one subapical tooth, the pygidial plate present in both sexes (that of the female rounded apically), and the gonostylus articulated. All those characters, with the probable exception of the parallel inner margins of eyes, are symplesiomorphies, their alternatives being apomorphies for *Osiris*. The recognition of *Protosiris* as a natural group is supported by the long, curved, sickle shaped mandible, unique among osirines. The parallel margins of the eyes also represent an apomorphy for the group in the context of the cladogram in figure 1.

The three species of *Osirinus* are small and have a similar habitus. They are differenti-

ated from *Osiris* and *Protosiris* by the stouter build of the body, short legs, inner margin of eyes almost straight and convergent below, mandible short with one subapical tooth, and plumose vestiture dense at least on the mesopleuron, scutellum and tibiae. The type species is strikingly hairy, with wide bands of plumose hairs on the metasomal terga. Most of these characters represent plesiomorphies; undoubtedly *Osirinus* is close to the ancestral stock that gave rise to the *Osirinus-Protosiris-Osiris* branch. The short legs, shorter than in any other osirines, may represent a synapomorphy. There are some characters that seem to have arisen independently in the three genera: reduction of the maxillary palpus and loss of the volsella. *Osirinus* and *Osiris* are characterized by a maxillary palpus with 5 segments, *Protosiris* has species with 4 to 6 segments. Species of *Osiris* and the only species of *Osirinus* with known males do not have volsellae; in *Protosiris* there are species with and without volsellae.

## BIOLOGY

Knowledge of the biology of the Osirini is quite fragmentary and limited to a few host associations. *Epeoloides* is known to be parasitic in the nests of the melittid genus *Macropis*. The European *E. coecutiens* has been associated with *M. labiata* and *M. fulvipes* (Popov, 1958, and references therein). All other hosts are in the Exomalopsini. Rozen (1984) reported *Parepeolus niger* (mentioned as *Parepeolus sp.*) flying in association with *Tapinotaspis (Tapinotaspoides) tucumana* in southern Brazil; he found a female of the parasite inside a nest of *T. tucumana*. I collected a series of *Ecclitodes stuardi* in Chile (Cabrería, Malleco Province, 22-XII-1985) that were flying back and forth along a low, sunny

slope occupied by *Tapinotaspis (Tapinorhina) caerulea*. From time to time the parasites perched on nearby herbs or more frequently stayed still on the ground. I did not observe actual entrance of the parasites into the nests. H. Toro (personal communication) also found *Ecclitodes* in association with *Tapinotaspis caerulea* in the province of Malleco, Chile (Nahuelbuta, 9-I-1979). The host relationships of *Osiris* are not known, but indirect evidence suggests *Paratetrapedia* and *Monoeca* as possible hosts (summarized in Shanks, 1986).

It is interesting to note that all recorded hosts of the osirines are known or suspected to be oil-collecting bees.

## TRIBE OSIRINI

Length 5.5-18 mm, with slender habitus when over 13 mm. Integument moderately punctate to almost impunctate, polished between punctures. Vestiture abundant and plumose to sparse and mostly simple. Labrum transverse with sides sharply bent backwards. Maxillary palpus with 4 to 6 segments. *Stipes* with longitudinal ridge on outer surface. Stipital comb developed, usually on edge

of distinct concavity. *Epistomal suture faded laterally near eye*. Preoccipital carina absent, except present behind ocelli in *Osiris*. *Cervical membrane with rounded ventral sclerite*. Axilla not projecting. *Forecoxa with ventral carina along inner and basal margins*, sometimes basal sector of carina short. Middle coxa slightly longer than distance from its summit to hind wing base. Claws usually with flat, square

inner tooth. Forewing with 3 submarginal cells. Pterostigma moderate to large, 3-8 times as long as prestigma. Jugal lobe of hindwing 0.2-0.4 times as long as vannal lobe measured from wing base. Abdomen depressed, moderately so in *Epeoloides*. T5 of female without pseudopygidial area, instead with wide, polished apical margin. S6 of female without spine-like setae, more or less boat-shaped

and pointed posteriorly; elongate in *Osiris*. Sting sometimes upcurved over metasoma. Pygidial plate usually present in both sexes. Male genitalia with gonobasal ring complete; gonostylus usually articulated, with a dorsal and a ventral branch; midapical lobe of gonocoxite present in *Ecclitodes* and *Parepeolus*, complex; spatha present, small.

KEY TO THE GENERA OF OSIRINI

- 1. Jugal lobe of hindwing rounded (fig. 10). Basal vein of forewing arising basal to cu-v or sometimes meeting it. Lateral margin of clypeus not continued above level of anterior mandibular articulation by paraocular carina (figs. 3, 12). Labrum with pair of preapical tubercles or 2-4 teeth near middle of disc (figs. 3, 12, 15). Genitalia of male with ventral ramus of gonostylus bifid, dorsal ramus flattened (figs. 7, 17, 19, 21) . . . . . 2
- Jugal lobe of hindwing elongate (fig. 23). Basal vein of forewing arising apical to cu-v or sometimes meeting it. Lateral margin of clypeus continued by paraocular carina above level of anterior mandibular articulation (figs. 25, 29, 33, 43, 53). Labrum with single preapical tubercle or several small preapical denticles (figs. 25, 33, 43, 53). Ventral ramus of gonostylus simple; dorsal ramus small, cylindrical or absent (figs. 40, 48) . . . . . 3
- 2. Metapostnotum microstriate. Posterior margin of first submarginal cell more than twice as long as apical margin (fig. 10). Maxillary palpus with 6 segments. Metasomal terga with apical bands of pale hairs. Supratergular carina curved cephalad of tegula, following regular margin, reaching mesoscutum-pronotal lobe boundary close to tegula . . . . . *Ecclitodes*
- Metapostnotum polished, smooth or with few scattered punctures. Posterior margin of first submarginal cell less than 1.5 times as long as apical margin (fig. 13). Maxillary palpus with 4-5 segments. Metasomal terga black or variously patterned with pale hairs; apical band, when present, only on T1. Supratergular carina slightly curved, directed anteriorly, diverging from regular margin and reaching mesoscutum-pronotal lobe boundary near middle (fig. 11) . . . . . *Parepeolus*
- 3. Apex of marginal cell curved away from wing margin (fig. 23). Paraocular carina almost reaching top of eye. Eyes of male strongly converging above, those of female slightly so. Labrum with strong preapical tubercle. Pterostigma moderate, 2.8-3.2 times as long as prestigma. Claws of male with rami similar and adjacent . . . . . *Epeoloides*
- Apex of marginal cell terminating close to wing margin (fig. 28). Paraocular carina fading as soon as it reaches lower margin of eye. Eyes of both sexes parallel or diverging above. Labrum with several small denticles. Pterostigma long, more than 5.5 times as long as prestigma. Inner ramus of male claws shorter than outer, flattened . . . . . 4
- 4. Collar of pronotum dorsally bulging, with distinct subhorizontal portion connecting rounded dorsolateral lobes. Inner margin of eye not straight, with shallow emargination near upper third (fig. 53). Mandible with two subapical teeth. S6 of female usually exceeding T6. Apex of pygidial plate of female not reaching margin of tergum; wide rim apical to plate present (fig. 51). Pygidial plate of male reduced to sclerotization on tergal margin . . . . . *Osiris*
- Transverse dorsal sector of pronotal collar short or absent medially, so that dorsolateral lobes are nearly connected. Inner margin of eye almost straight (figs. 29, 33, 43). Mandible with one subapical tooth or simple (an inner angle may be present). S6 of female not exceeding T6. Apex of pygidial plate of female constituting apex of tergum (figs. 36, 38, 50). Pygidial plate of male present . . . . . 5
- 5. Inner margins of eyes almost parallel; proportion of lower to upper interocular distance 0.97-1.03:1. Mandible long, strongly curved (fig. 44, 47); outer basal width 0.33-0.35



times length of mandible (measured along dashed line shown in figure 44). Mesopleuron with hairs simple or at most with one or two basal barb. Legs slender; strigular concavity 0.26-0.27 times length of forebasitarsus (fig. 46). Scutum as long as intertegular span .

- ..... *Protosiris*  
 —. Inner margin of eyes convergent below; proportion of lower to upper interocular distance 0.82-0.90:1. Mandible short (fig. 33); outer basal width 0.4-0.45 times length of mandible. At least anterior part of mesopleuron with plumose hairs. Legs short, stout; strigular concavity shallow, 0.38-0.41 times length of forebasitarsus (fig. 32). Scutum shorter than intertegular span ..... *Osirinus*

### *Ecclitodes*, new genus

(figs. 2-10)

Type species: *Epeolus stuardi* Ruiz, 1935.

*Ecclitodes* includes bees with black and pale, silvery hairs, head robust with a wide gena, and depressed metasoma. It is distinguished from the closely related *Parpeolus* by the *metapostnotum* with *microstriae*, the *metasoma* with *apical bands of pale hairs on T1-T5*, the *disc of the labrum with two blunt preapical tubercles*, and the apex of the marginal cell slightly truncate, usually briefly appendiculate.

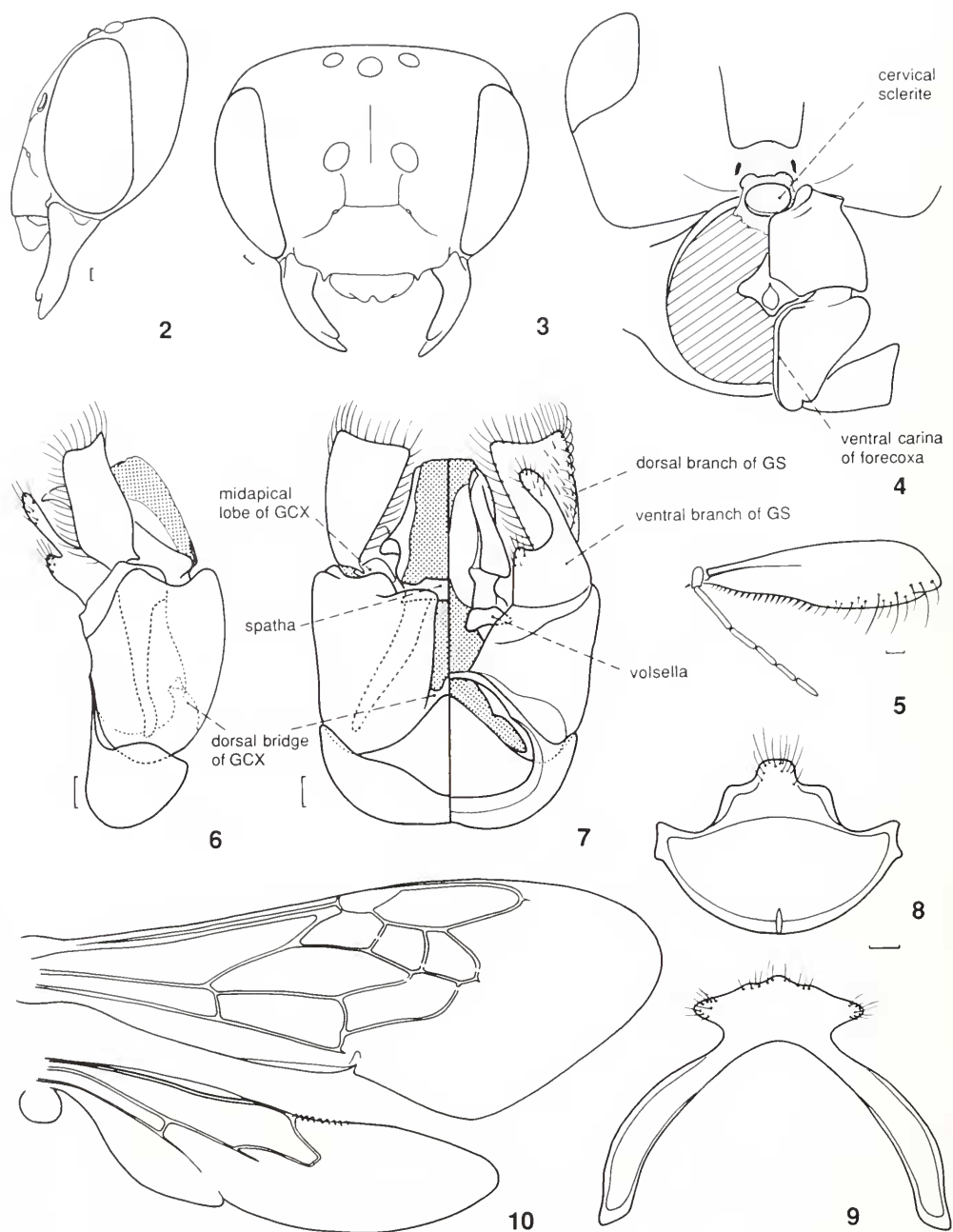
*Description.* 1. Length 8.5-10.5 mm. 2. Integument black; flagellum, mandible and tarsi sometimes red. 3. Mesopleura with dense, small punctures, those on scutum extremely fine; metapostnotum microstriated, striae running parallel to metanotum at sides, curving medially and then running parallel to longitudinal sulcus; parts of metapostnotum not striated with fine, close punctures. 4. Vestiture long and plumose on head, mesosoma and legs; metasoma with apical tergal fasciae of appressed plumose hairs. 5. Eyes convergent below, proportion of lower to upper interocular distance 0.75:1; inner margin of eye almost straight. 6. Lateral ocellus separated from posterior margin of head by 1.5 ocellar diameters. 7. Maximum width of gena 0.75 times maximum width of eye seen from side; gena slanting toward base of mandible. 8. Preoccipital and paraocular carinae absent. 9. Short malar space present, 0.15 times as long as basal width of mandible. 10. Disc of labrum with two close, blunt, preapical tubercles. 11. Mandible with one subapical tooth. 12. Stipital comb-bearing concavity absent. 13. Maxillary palpus with 6 segments. 14. Hypostomal carina forming rounded angle near mandibular socket. 15. Proportion of first to second flagellomere 0.8-1.0:1. 16. Pronotum not forming raised collar; anterior dorsal margin not recurved. 17. Scutum shorter than intertegular span (approximately 0.8). 18. Suprateregular carina curving anteriorly close to tegula. 19. Apex of marginal cell curved away from wing margin, sometimes briefly appendiculate. 20. Prestigma approximately 1.5 times as long as wide; pterostigma 3 times as long as prestigma. 21. First submarginal cell with posterior margin straight, 2.2-2.8 times as long as apical margin. 22. Basal vein of forewing arising basal to vein

cu-v. 23. Jugal lobe of hindwing rounded, 0.2 times as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina short, restricted to third. 25. Legs short, stout; external surface of hindtibia densely hairy; strigular concavity of forebasitarsus 0.38 times as long as segment. 26. Metapostnotum usually with basal subhorizontal zone, but some specimens with metapostnotum declivous, more or less convex. 27. Pygidial plate present in both sexes. 28. Genitalia as in figures 6, 7; ventral branch of gonostylus bifid, dorsal branch flattened, not larger than ventral branch; apodeme of penis valve more or less straight; volsella present.

*Comments.* This genus has been recognized by various authors in the past, but has never been described. I have seen names on labels by Brèthes, Moure and Moldenke; I have chosen the oldest one, written on labels by Brèthes. The root *ekklites* means "the one who doesn't like to work," a name quite appropriate for a parasitic bee.

Two series of specimens from nearby areas in the province of Malleco (Chile) each contain specimens that are easily separated into two forms by the features mentioned below. These two forms may represent a single dimorphic species or else two sympatric ones. I am inclined toward the second alternative, since the differences are clear and hold in the few specimens that I have examined from other areas. On the other hand, there is only one suspected host for the two putative species. Both host and parasites need to be studied in more detail to solve this problem.

Specimens that I have identified as *stuardi* agree better with the color pattern described by Ruiz: antenna brownish, mesothorax with patches of black and silvery hairs, last metasomal segment of female black. The second species has light red antennae, mesothorax mostly covered with pale hairs and sixth tergum of female with pale hairs, too. Since there is some variation in the extent of the pale hairs, the identification is tentative. Other features mentioned by Ruiz fit both forms. Study of the types or material from the type locality (Termas de Chillán, Ñuble) will allow clarification of this point. Females that I regard as



Figs. 2-10. *Ecclitodes stuardi*; 2-5 and 10, female; 6-9, male. 2, head, lateral. 3, face. 4, ventral view of head and prothorax; right half of prosternum and right coxa removed. 5, stipes. 6, genitalia, lateral. 7, genitalia, dorsal and ventral. 8, sternum 8. 9, sternum 7. 10, wings. Scale lines 0.1 mm. GCX = gonocoxite; GS = gonostylus.

*stuardi* have a triangular pygidial plate with sides converging at an angle of 30 degrees and males have the dorsal branch of the gonostylus with the inner apex not lobed. The other species presents a strikingly narrowed pygidial plate in the female and the male gonostylus has a lobed dorsal branch. There is variation in the shape of the metapostnotum. It usually has a basal sub-horizontal zone, but in some specimens it is more or less declivous. There is no correlation between this variation and the set of characters mentioned above.

I have studied material from the provinces of Malleco, Cautín and Valdivia in Chile and from the province of Rio Negro in Argentina.

**Parepeolus** **Ducke**

*Parepeolus* Ducke, 1912: 71, 102. Type species: *Leipodius lecointei* Ducke, 1907 (= *Epeolus aterrima* Friese, 1906), by designation of Sandhouse, 1943: 585.

*Parepeolus* is distinguished by the polished metapostnotum; the suprategular carina directed anteriorly, slightly curved; the metasoma depressed, variously patterned, but with an apical band of pale hairs only on T1; the apex of the marginal cell usually broadly rounded; and the dorsal branch of the male gonostylus flat, strikingly large.

*Description.* Agreeing with *Ecclitodes*, except as follows: 1. Length 6-13 mm. 2. Integument black

to dark reddish brown. 3. Punctures of mesopleura from small and dense to extremely fine; metapostnotum always impunctate and shiny. 4. Vestiture of metasoma short, appressed, variously patterned with black and pale hairs. 5. Proportion of lower to upper interocular distance 0.67-0.79:1. 6. Lateral ocellus separated from posterior margin of head by 1-2.3 ocellar diameters. 9. No malar space. 10. Labrum with transverse carina near middle, bearing at least two teeth, usually four. 12. Stipital comb-bearing concavity present, or concavity reduced. 13. Maxillary palpus with 4 to 5 segments. 15. Proportion of first to second flagellomere 0.75-1.75:1. 18. Suprategular carina slightly curved, directed anteriorly, reaching boundary of scutum with pronotal lobe near middle. 19. Apex of marginal cell rounded, away from wing margin. 20. Prestigma 1-1.4 times as long as wide; pterostigma 3-4 times as long as prestigma. 21. Posterior margin of first submarginal cell 0.95-1.5 times as long as apical margin. 22. Basal vein arising basal to vein cu-v or meeting it. 26. Metapostnotum entirely declivous. 28. Genitalia as in figures 17, 19, 21; dorsal branch of gonostylus flattened, larger than ventral branch.

*Comments.* Four species are recognized in *Parepeolus*, two of them known from only one sex. Since there is little sexual dimorphism in the punctuation and structure of *aterrimus* and *niger*, I expect that the unknown sexes of *minutus* and *laticeps* will be easily associated when discovered.

KEY TO THE SPECIES OF PAREPEOLUS

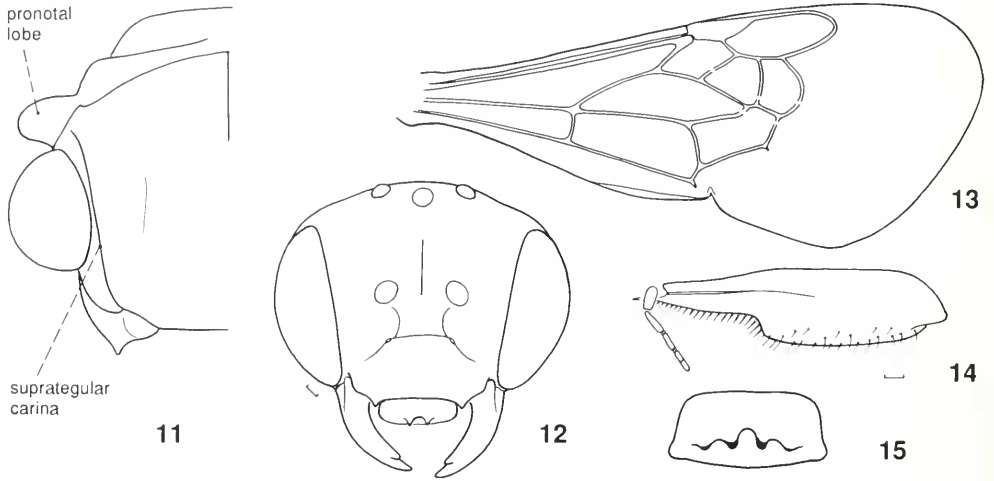
Females

- 1. Patches of pale hairs yellowish to light brown. Scutellum at each side of median line with tuft of erect, plumose, brownish hairs, longer than third flagellomere. Labrum with two teeth near middle of disc (fig. 12). Mesepisternum polished, with scattered small punctures barely twice diameter of hairs arising from them. Forewing hyaline with apex dark. Length 6mm . . . . . *minutus*
- Patches of pale hairs white, or hairs wholly black. Scutellum with plumose hairs mostly appressed, shorter than third flagellomere. Disc of labrum with carina bearing 4 teeth (fig. 15). Mesepisternum with punctures distinct. Forewing usually black, partly hyaline in specimens of *aterrimus* from northern Brazil. Length 7.5-13 mm . . . . . 2
- 2. Face and body in general with dense hairs hiding integument. Mesepisternum with dense punctures, below scrobe less than a diameter apart. Propodeal spiracle surrounded by punctures, those behind spiracle as large as those on mesepisternum. Proportion of first to second flagellomere 0.75-1:1. Pygidial plate with distinct punctures bearing short setae . . . . . *aterrimus*
- Face and body in general with sparse hairs not hiding shiny integument. Punctures on mesepisternum more than one diameter apart. Integument around propodeal spiracle mostly smooth and shiny; if fine punctures behind, then much smaller than those of mesepisternum. Proportion of first to second flagellomere 1.25-1.5:1. Pygidial plate finely sculptured, without punctures or short setae . . . . . *niger*

Males

- 1. S6 with apical, central patch of short hairs and lateral brushes of long, dense hairs separated from margin of segment by polished area, together forming sinuous fringe, arched at sides. Genitalia, fig. 19 . . . . . *aterrimus*

- S6 without lateral brushes of long, dense hairs . . . . . 2
- 2. Lateral ocellus separated from posterior margin of head by 2.3 ocellar diameters. Scutellum slightly bigibbous. Flagellomeres 3-6 each with small subapical tubercle on polished underside; these tubercles of equal size. Genitalia, fig. 21 . . . . . *laticeps*
- Lateral ocellus separated from posterior margin of head by 1.15-1.40 ocellar diameters. Scutellum evenly convex. Flagellomeres 4-6 each with small subapical tubercle on underside, that on flagellomere 4 more conspicuous. Genitalia, fig. 17 . . . . . *niger*



Figs. 11-15. *Parepeolus*, females. 11, *P. aterrimus*, left half of pronotum and scutum. 12, *P. minutus*, holotype, face. 13, *P. niger*, holotype, forewing. 14, *P. aterrimus*, stipes. 15, *P. aterrimus*, labrum. Scale lines 0.1 mm.

***Parepeolus aterrimus* (Friese), new combination**  
(figs. 11, 14-16, 19-20)

*Epeolus aterrima* Friese, 1906: 101. Type male from Mendoza, Argentina, Jensen-Haarup coll. (not examined); Friese, 1908: 81, 82; Jörgensen, 1909: 219, 225.

*Epeolus aterrima fuscipennis* Friese, 1906: 101. Male and female types from Tucumán, Argentina, 2000 m, Steinbach coll. (not examined). **New synonymy.**

*Leiopodus lecoitei* Ducke, 1907: 88. Lectotype female, by present designation, from Lago Grande de Vilafranca, Pará, Brazil, Lecoite coll. (Mus. Berlin, examined); Ducke, 1908a: 103-104; Ducke, 1908b: 79. **New synonymy.**

*Leiopodus gigas* Friese, 1908: 91. Holotype male from Jundiahy, São Paulo, Brazil, 17 November (Mus. Berlin, examined). **New synonymy.**

*Epeolus lecoitei*: Ducke, 1910: 104.

*Isepeolus aterrimus*: Jörgensen, 1912a: 142; 1912b: 316.

*Parepeolus lecoitei*: Ducke, 1912: 102; Sandhouse, 1943: 585.

*Parepeolus gigas*: Ducke, 1912: 102.

*P. aterrimus* can be distinguished from the other species of *Parepeolus* by the dense punctures of similar size on the mesepisternum and the propodeum, the first flagellomere usually shorter than the second (proportion of the first to the second flagellomere 0.75-1.10:1), the maxillary

palpus with 5 segments, the disc of the pygidial plate in the female with distinct punctures bearing short setae, the disc of the pygidial plate in the male covered with hairs, and the distinctive lateral brushes on S6 of the male.

This species shows considerable variation in the pattern of pale hairs and the color of the wings. Specimens from northern Brazil have extensive white maculations; specimens from central and western Argentina are wholly black (fig. 16). The lectotype of *lecoitei*, at one extreme of this variation, has the following areas with white hairs: frons, labrum, gena, pronotal band including the pronotal lobes, two anterior patches on scutum, most of scutellum, metanotum, upper half of the mesepisternum, propodeum, outer sides of legs, most of T1 except two subapical black spots, lateral spots on T2, T5 and T6, lateral and central spots on T3 and T4 and small latero-apical spots on S2-S5. These patches may be reduced or absent in specimens from other areas. The lectotype of *lecoitei*, as well as specimens from the states of Ceará and Bahia in Brazil, have at least the basal half of the forewing hyaline; specimens from elsewhere have the fore-

wing entirely black. I have not found any morphological characters, including the genitalia, suggesting that this is not a single species.

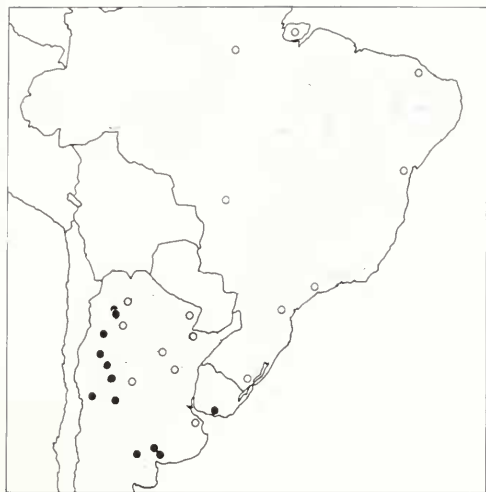


Fig. 16. Distribution of *Parepeolus aterrimus*. Open circles represent specimens with patches of white pubescence; dots represent specimens with pubescence wholly black.

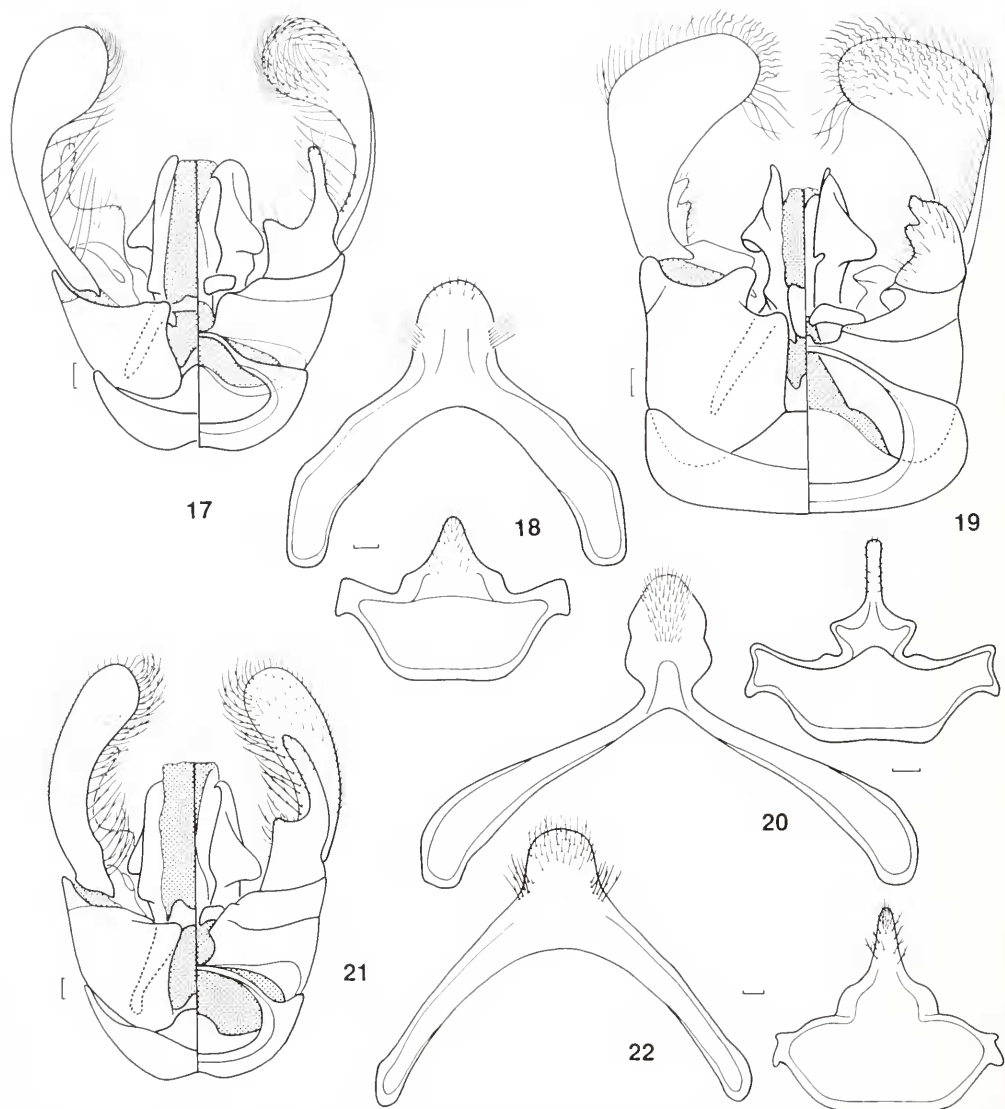
I have not seen the types of *aterrimus* or *fuscipennis*, but Friese's original descriptions do not leave doubt about their identity. He mentions for *aterrimus* the shape of the fringe of hairs of S6 of the male, diagnostic for the species; *fuscipennis* is described as a color variant of the former. *P. lecointei* was described from both sexes in a key, the intended original description, more detailed, appeared one year later (Ducke, 1908a). The selected lectotype is the only specimen that I have studied from the original series. *Leiopodus gigas* Friese is a further synonym. The size of the holotype falls within the range of the species (8-12.5 mm long); it does not differ from males of *aterrimus* in any significant respect.

I have studied material from the states of Pará, Ceará, Bahia, Mato Grosso, São Paulo, Paraná and Rio Grande do Sul in Brazil, from Montevideo in Uruguay and from the provinces of Formosa, Corrientes, Santa Fe, Córdoba, Tucumán, Salta, Catamarca, La Rioja, Mendoza, San Luis, La Pampa and Buenos Aires in Argentina (fig. 16). Collection dates in northern Brazil are June, July and February; in southeastern Brazil, December and January; in Uruguay and Argentina, November to March.

*Parepeolus niger*, new species  
(figs. 13, 17-18)

This species can be distinguished by the punctuation of the mesepisternum, coarser than that of the propodeum; the first flagellomere 1.25-1.7 times longer than the second; the forewing with basal vein and cu-v meeting; the pygidial plate in both sexes without distinct punctures; and flagellomeres 4-6 in the male each with a small subapical tubercle, that on flagellomere 4 larger than the other two.

*Female*. Length 8-11 mm (holotype 8.8); length of forewing 6-7.2 mm (holotype 6.6). Integument black; apex of mandible reddish; flagellum on underside brownish; pronotal lobe, tegula, legs and metasoma dark reddish brown to black. Forewing deeply infuscated; hindwing infuscated on apical half, base hyaline. *Vestiture*. Pubescence of head, thorax and propodeum black, some specimens, including holotype, with white hairs on supraclypeal area and upper half of clypeus; few specimens with hairs on propodeum white. Hairs of mesepisternum and propodeum long, plumose; those of scutellum mostly appressed, but some stiff, erect hairs present. Pubescence of legs black, except apical white spot on hindcoxa; external surface of hindtibia with dense, plumose white hairs on apical two thirds (holotype) (some specimens with legs wholly black). Pubescence of metasoma black with following pattern of white hairs: T1 with apical band notched medially and expanded laterally; T2-T4 with lateroapical spots (holotype), some specimens with lateroapical spots on T5 too, others with T2-T5 wholly black. *Sculpture*. Face shining, punctures on clypeus and paraocular areas minute; mesepisternum with distinct punctures, below scrobe clearly more than one diameter apart, leaving shiny interspaces; densest punctures close to anterior border of mesepisternum, nearly one diameter apart; lower third of metapleura polished, above with minute punctures; propodeum shiny, around spiracle without punctures or with punctures behind spiracle much smaller than those of mesepisternum; metapostnotum polished, impunctate; pygidial plate finely sculptured, without punctures or setae. *Morphology*. Proportion of lower to upper interocular distances 0.78-0.80:1. Lateral ocellus separated from posterior margin of head by 1.1-1.3 ocellar diameters. Labrum 0.43-0.48 times as long as wide, with transverse, arched carina on apical third that bears 4 teeth, the central ones stronger. Maxillary palpus with 4 segments. Proportion of first to second flagellomere 1.25-1.50:1; of second to third 0.9-1.0:1. Scutellum evenly convex. Basal vein of forewing meeting cu-v; in one specimen briefly basad. Pterostigma 2.75-3.5 times as long as prestigma; second submarginal cell longer than first or third; proportion of lengths on posterior margin 0.7-0.95:1:0.55-0.75. Posterior margin of first submarginal cell 0.9-1.3 times as long as apical margin.



Figs. 17-22. *Parepeolus*, males. *P. niger*: 17, genitalia, dorsal and ventral; 18, sterna 7 and 8. *P. aterrimus*: 19, genitalia, dorsal and ventral; 20, sterna 7 and 8. *P. laticeps*, holotype: 21, genitalia, dorsal and ventral; 22, sterna 7 and 8. Scale lines 0.1 mm.

*Male*. Length 7.5-10 mm; length of forewing 6.5-7.5 mm. Color, vestiture and punctuation similar to those of female, but some specimens with white appressed hairs on face from above antennal sockets to apex of clypeus and white hairs on external surface of mid and hindtarsi; metasomal sterna sometimes with poorly defined subapical bands of white hairs and fringes on S3-S5 white; other specimens with sterna entirely black. *Morphology*. Proportion of lower to upper interocular distance 0.73-0.80:1. Lateral ocellus separated from posterior margin of head by

1.15-1.40 ocellar diameters. Proportion of first to second flagellomere 1.3-1.7:1, second and third of same length. Flagellomeres 4-6 each with small subapical tubercle on underside; tubercle on flagellomere 4 more conspicuous. Disc of pygidial plate polished, without hairs or punctures. Apex of S6 with central patch of short hairs bordered by polished lateral areas. Genitalia, figure 17.

*Comments*. This species was recognized and named on labels by J. S. Moure; I am using the name that he proposed. Specimens from Argentina have more extensive areas of white hairs;

most specimens from Brazil are entirely black except for the apical band on T1. This distribution of pale and dark forms is the converse of the geographic variation seen in *P. aterrimus*.

*Material studied.* Holotype female from El Sauce, Dpto. Calamuchita, Prov. Córdoba, Argentina, XII-1938, M. J. Viana (MACN). Paratypes: ARGENTINA: Jujuy: 1 male, Jujuy, Spegazzini coll. (MACN). Tucumán: 1 female, San Pedro de Colalao, II-1949, Arnau (SEM); 1 male, San Pedro de Colalao (UFPR). Córdoba: Agua de Oro, I-1940, J. A. de Carlo (SEM). PARAGUAY: 1 male, SW Saltos del Guayra, Paraná, 8-XII-1971, L. Peña (AMNH). BRAZIL: Paraná: 3 females, 4 males, Villa Velha, 20-I-5-II-1974, J. G. Rozen, F. C. Thompson and J. S. Moure (1 female, 1-II-1974, with indication "nest", specimen referred to by Rozen, 1984) (AMNH); 2 females, 1 male, Rio Negro, 7-II-1974, J. G. Rozen and F. C. Thompson (AMNH). São Paulo: 1 female, Mogi-Guaçu, 23-I-1974, J. G. Rozen, F. C. Thompson and J. S. Moure (AMNH).

*Parepeolus laticeps*, new species

(figs. 21, 22)

This species is allied to *niger*, from which it is distinguished by the broader vertex (hence the specific name), the slightly bigibbous scutellum, the finer punctation of the mesepisternum, the number and size of the flagellar tubercles and the shape of the gonostylus.

*Male.* Length 13 mm; length of forewing 10.3 mm. Integument black; apex of mandible reddish. Wings deeply infuscated except pale basal third of hindwing and pale longitudinal line crossing submarginal cells. *Vestiture.* Pubescence of head black; a few pale hairs above antennal sockets. Thorax with black hairs, those on mesepisternum long, plumose; those on scutellum mostly appressed, some scattered, erect, stiff. Propodeum with long, plumose, white hairs. Legs mostly with black hairs, but white hairs as follows: foredistantarsus above; external surfaces of mid and hindtarsi; apical third of midtibia; most of hindtibia and apical spot on mid and hindcoxae. Hairs on hindtibia strikingly dense. Pubescence of metasoma black including apical fringes of S4-S5; with following pattern of white hairs: T1 with apical band expanded medially and laterally, forming two dark preapical spots, T2 with large lateral spot, T3-T6 with apicolateral spots, small on T3 and T6, moderate on T4-T5. *Sculpture.* Integument of head and thorax shiny, with fine, fairly dense punctures; mesepisternum with small punctures, more than one diameter apart below scrobe; metapleura with minute punctures, except lower fourth; propodeum shiny, before spiracle without punctures, behind spiracle with fine punctures similar to those of mesepisternum. Metapostnotum polished, impunctate. *Morphology.* Proportion of

lower to upper interocular distances 0.84:1. Lateral ocellus separated from posterior margin of head by 2.3 ocellar diameters. Labrum 0.43 times as long as wide; with transverse carina near middle bearing 4 teeth, central ones stronger. Maxillary palpus with 4 segments. Proportion of first to second flagellomere 1.75:1, of second to third 0.9:1. Flagellomeres 3-6 each with small subapical tubercle on underside; tubercles equal in size. Scutellum slightly bigibbous. Basal vein of forewing meeting vein cu-v. Pterostigma 3 times as long as prestigma. Proportion of lengths of submarginal cells along posterior margin 0.8:1:0.63. Posterior margin of first submarginal cell 0.97 times as long as apical margin. Disc of pygidial plate polished, without punctures or hairs. Apex of S6 with central patch of short hairs bordered by polished lateral areas. Genitalia, fig. 21; dorsal branch of gonostylus slightly swollen distally; long hairs plumose.

*Material studied.* Holotype male from Itá Ibaité (Alto Paraná), Prov. Corrientes, Argentina, March 1962 (MACN).

*Parepeolus minutus*, new species

(fig. 12)

This species is the smallest in the genus. It can be distinguished by the yellowish brown color of the maculations, the fine punctation, the labrum with only two teeth, and the two tufts of erect hairs on the scutellum. The specific name refers to the small size.

*Female.* Length 6 mm; length of forewing 4.8 mm. Integument black; mandibles reddish except base; legs dark reddish brown. Wings slightly infuscated with apex dark beyond closed cells; marginal cell dark along anterior half. *Vestiture.* Pubescence of head sparse, black; face above and around antennal sockets with whitish, plumose hairs intermixed with black, stiff, almost simple hairs. Pubescence of thorax black with following pattern of yellowish brown hairs: posterior margin of pronotum with band not reaching pronotal lobes; anterior margin of scutum with lateral patches and small notaular spots; posterior margin of scutum with lateral patches joining band of scutellum; scutellum including axilla and metanotum with golden brown hairs, those on scutellum at each side of median line long, erect, plumose, darker at tips, forming distinct tuft. Propodeum with whitish, plumose hairs. Pubescence of legs black, except white spot on apical third of hindtibia. Pubescence of metasoma black with following areas yellowish brown: T1 with apical band, T2-T4 with short latero-apical bands expanded basally at sides, T5 with roundish paramedian patch that leaves central black eyespot. Posterior margins of S2-S5 with small lateral whitish spots. *Sculpture.* Integument of head and thorax shiny, with fine, sparse punctures; mesepisternum with widely separated punctures as small as those on clypeus and propodeum; metapleura with minute punctures; metapost-

notum shiny, impunctate; propodeum shiny, around spiracle with scattered punctures. *Morphology*. Proportion of lower to upper interocular distance 0.70:1. Lateral ocellus separated from posterior margin of head by 1.3 ocellar diameters. Labrum 0.5 times as long as wide, with 2 teeth near middle; beyond teeth longitudinal depression reaches apical margin. Maxillary palpus with 4 segments. Proportion of first to second flagellomere 1.08:1, of second to third 1:1. Scutellum evenly convex, although tufts of hairs give impression of bigibbousness. Basal vein of forewing arising basal to vein cu-v by distance equal to 3 times thickness of basal vein. Pterostigma 3.8 times as long as prestigma. Proportion of lengths of submarginal cells along posterior margin 0.83:1:0.83. Posterior margin of first submarginal cell 1.3 times as long as apical margin. Pygidial plate finely sculptured, without punctures or setae.

*Material studied*. Holotype female, 17 km E Magdalena, Prov. Buenos Aires, Argentina, 16-XI-1985, L. Moffatt (MACN).

### Genus *Epeoloides* Giraud

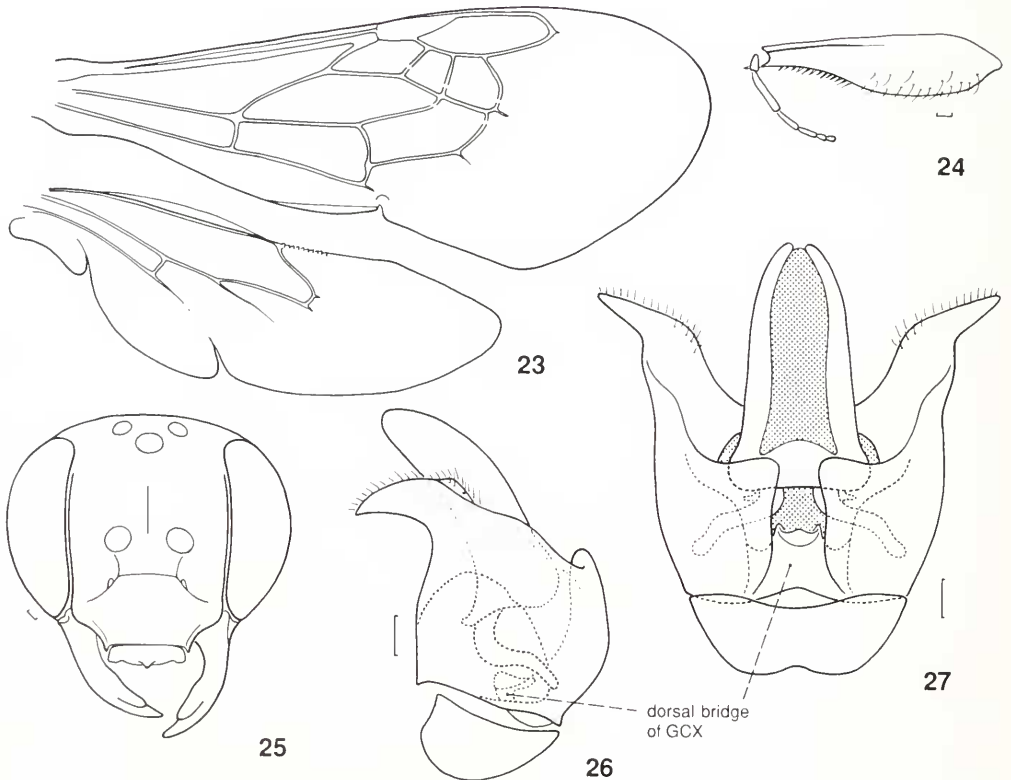
(figs. 23-27)

*Epeoloides* Giraud, 1863:45. Type species: *Epeoloides ambiguus* Giraud, 1863 (= *Apis coecutiens* Fab., 1775), by monotypy.

*Viereckella* Swenk, 1907: 298. Type species *Viereckella obscura* Swenk, 1907, by original designation.

*Epeoloides* is distinguished by the long and plumose vestiture, the eyes of the male strongly converging above, the paraocular carina almost reaching the top of the eyes, the labrum with a single preapical tubercle, the shiny metapostnotum with scattered plumose hairs, the claws of the male with the rami adjacent and similar, and the spatulate pygidial plate of the male.

Linsley and Michener (1939) presented a detailed generic description. The statements below are included to complement that description and to facilitate comparison with the other genera described here.



Figs. 23-27. *Epeoloides coecutiens*, female: 23, wings; 24, stipes. *Epeoloides pilosula*, female: 25, face. *Epeoloides pilosula*, male: 26, genitalia, lateral; 27, genitalia, dorsal. Scale lines 0.1 mm.



*Description.* 1. Length 7-9.5 mm. 5. Eyes of female slightly converging above; proportion of lower to upper interocular distance 1.04-1.1:1; inner margin of eye slightly concave. Eyes of male strongly converging above; proportion of lower to upper interocular distance 1.25-1.54:1. 11. Mandible with one subapical tooth, inner angle may be present. 12. Stipital comb-bearing concavity absent. 13. Maxillary palpus with 6 (*coecutiens*) or 4 segments (*obscura*, *pilosula*). 14. Hypostomal carina forming rounded angle near mandibular socket. 15. Proportion of first to second flagellomere dimorphic, in females 0.5-0.8:1, in males 1.0-1.25:1. 17. Scutum shorter than intertegular span (0.8-0.9). 18. Supratregular carina anteriorly curving close to tegula. 20. Prestigma twice as long as wide; pterostigma 2.8-3.2 times as long as prestigma. 23. Jugal lobe of hindwing elongate, 0.3-0.4 times as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina running completely across the coxa. 28. Genitalia, figures 26, 27.

***Osirinus*, new genus**

Type species: *Osirinus lemniscatus*, new species.

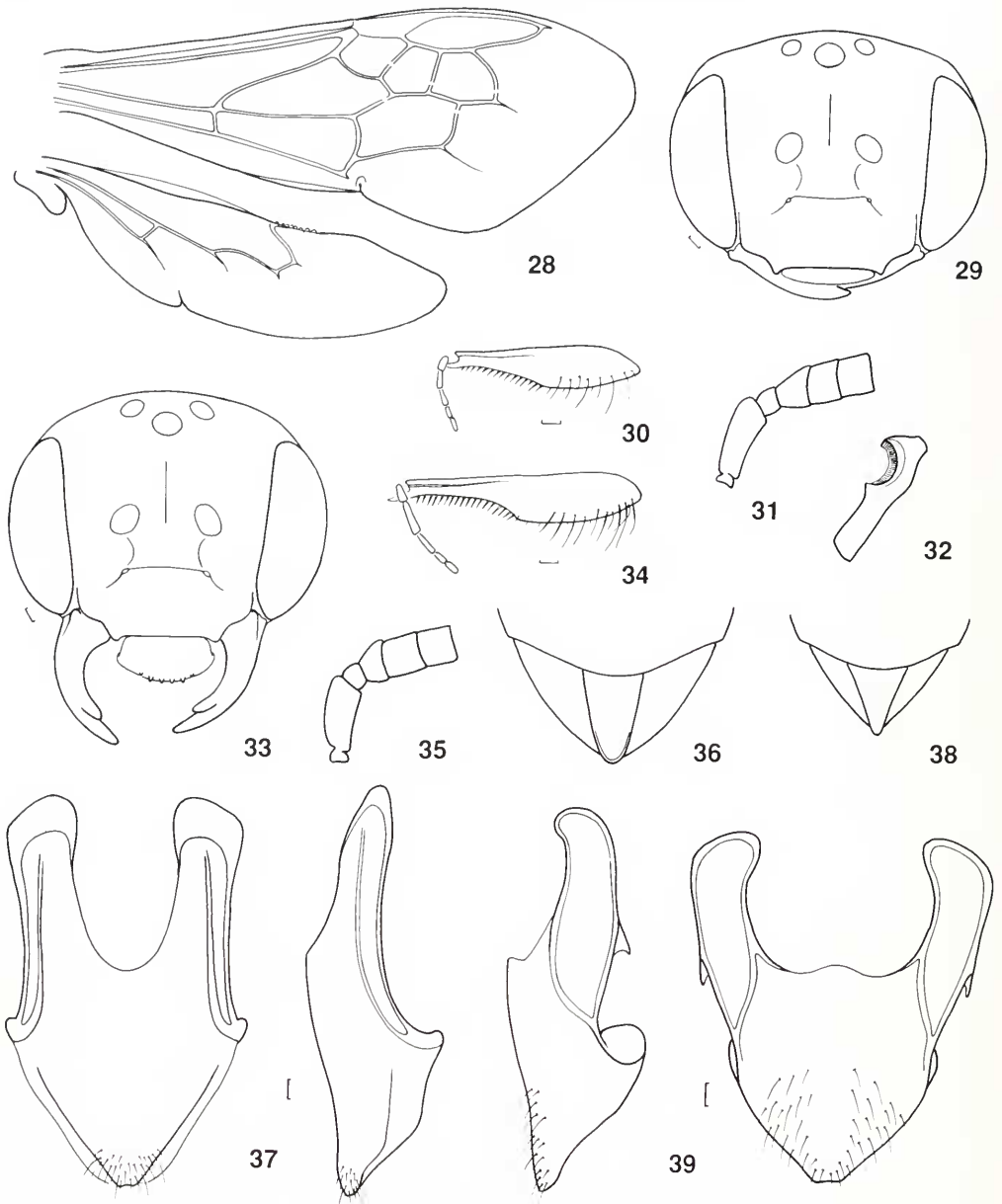
*Osirinus* shares with *Osiris* and *Protosiris* the shiny integument, pointed marginal cell, flat labrum with small preapical denticles, and the bowed posterior margin of the first submarginal cell. It is distinguished by the *plumose vestiture*, the *stout, short legs*, and the *eyes diverging above with the inner margins almost straight*.

*Description.* 1. Length 5.5-10 mm. 2. Integument black, patterned with red, to entirely testaceous. 3. Integument shiny; metapostnotum shiny, with or without hairs laterally. 4. Vestiture of head, mesosoma and legs consisting of long, plumose hairs; metasomal terga basally fasciate to almost bare. 5. Eyes convergent below, proportion of lower to upper interocular distance 0.82-0.90:1; inner margins of eyes almost

straight. 6. Lateral ocellus separated from posterior margin of head by 1.1-1.6 ocellar diameters. 7. Maximum width of gena 0.5-0.7 times as wide as maximum width of eye seen from side. 8. Preoccipital carina absent; paraocular carina short, continuing lateral margin of clypeus. 9. Malar space absent. 10. Labrum with 2 or more small preapical denticles. 11. Mandible with one subapical tooth; inner angle may be present. 12. Stipital comb-bearing concavity present. 13. Maxillary palpus with 5 segments. 14. Hypostomal carina forming rounded angle near mandibular socket. 15. Proportion of first to second flagellomere 0.55-1.2:1. 16. Pronotum not forming raised collar; dorsolateral lobes may be globose, but without median subhorizontal portion connecting them; anterior dorsal margin not recurved; posterolateral margin not emarginate below pronotal lobe. 17. Scutum shorter than intertegular span (0.78-0.9). 18. Supratregular carina curving anteriorly close to tegula. 19. Marginal cell pointed, apex close to wing margin. 20. Prestigma as long as or slightly longer than wide; pterostigma 5.6-6.0 times as long as prestigma. 21. First submarginal cell with posterior margin arched, 1.1-1.6 times as long as apical margin. 22. Basal vein of forewing meeting or arising apical to vein cu-v. 23. Jugal lobe of hindwing elongate, 0.22-0.25 times as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina complete, running all across the coxa. 25. Legs short, stout; hindtibia usually with stiff, broad setae intermixed with slender ones; strigular concavity of forebasitarsus 0.38-0.41 times as long as segment. 26. Metapostnotum with differentiated basal sector or entirely declivous. 27. Pygidial plate present in both sexes. 28. Genitalia as in figures 40, 41 (male known only for *O. lemniscatus*). Ventral branch of gonostylus not articulated, dorsal branch cylindrical, articulated; apodeme of penis valve strongly curved; volsella absent.

KEY TO FEMALES OF OSIRINUS

- 1. T2-T4 with broad basal bands of plumose, appressed, yellowish hairs. Scutellum with tuft of erect hairs at each side of median line. Integument mostly dark. Forewing infusate, with conspicuous subapical hyaline spot; pterostigma yellowish. Proportion of first to second flagellomere 0.86-1:1 (fig. 31). Metapostnotum with basal, central depression and lateral patches of appressed hairs . . . . . *lemniscatus*
- T2-T4 almost bare. Scutellum with erect hairs not forming tufts. Integument mostly reddish to pale yellowish brown. Forewing evenly infusate; pterostigma dark. Proportion of first to second flagellomere 0.55-0.6:1 (fig. 35). Metapostnotum bare, entirely declivous . . . . . 2
- 2. Apex of pygidial plate acute, spot on disc evident (fig. 38). Hindtibia without differentiated, stiff setae. Labrum with two preapical denticles separated by short longitudinal depression. Posterior margin of first submarginal cell 1.6 times as long as apical margin . . . . . *rutilans*
- Apex of pygidial plate rounded, no spot evident on disc (fig. 36). Hindtibia with stiff, basally broad and apically curved setae along dorsal margin. Labrum with row of 6 preapical denticles. Posterior margin of first submarginal cell 1.25 times as long as apical margin . . . . . *fritzi*



Figs. 28-39. *Osirinus lemniscatus*, female: 28, wings; 29, face; 30, stipes; 31, basal segments of antenna; 32, forebasitarsus. *Osirinus fritzi*, female holotype: 33, face; 34, stipes; 35, basal segments of antenna; 36, T6 showing pygidial plate; 37, S6, ventral and lateral. *Osirinus rutilans*, female: 38, T6 showing pygidial plate. *Exomalopsis* sp., female: 39, S6, ventral and lateral. Scale lines 0.1 mm.

***Osirinus lemniscatus*, new species**

(figs. 28-32, 40-42)

This species is easily distinguished by its abundant plumose vestiture and dark integument, the basal bands of appressed hairs on the metasomal

terga (unique in the tribe), the hyaline subapical spot on the forewing and the subequal first and second flagellomeres.

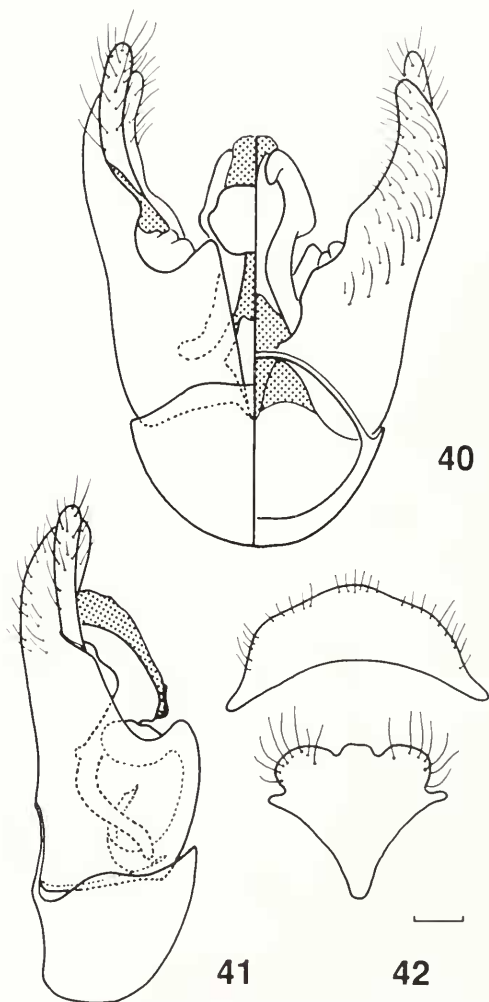
*Female*. Length 5.5-10 mm (holotype 6.0); length of forewing 4.8-7.4 mm (holotype 5.0). Head black with reddish, elongate spot between

lateral ocellus and eye, reddish spot on gena near upper corner of eye, and some specimens with apex of clypeus and labrum reddish; mandible reddish except base. Scape dark with base brownish; pedicel and flagellum light brown, sometimes with longitudinal dark band. Thorax black to dark reddish brown, with following parts yellowish brown to reddish brown: pronotal lobes, antero-lateral angles and posterior margin of scutum, scutellum including axilla, middle of metanotum, and upper part of mesepisternum excluding hypopimeral area (some specimens with mesepisternum entirely black). Propodeum black. Legs dark reddish brown; apices of femora, usually apices and bases of tibiae, and most tarsomeres light brown (hindtibia sometimes entirely so). Metasoma dark reddish brown to black; pygidial plate light brown. Forewing infusate, with irregular hyaline spot surrounding third intercubitus and second recurrent vein, feebly connected with smaller hyaline spot behind second submarginal cell; in some specimens cells paler medially; pterostigma yellowish, veins brown. Hindwing hyaline with apex infusate. *Vestiture*. Hairs plumose. Hairs on head mostly brown, whitish around antennal socket and on vertex behind ocelli. Thorax with intermixed whitish and brown hairs, short, appressed on scutum, long, erect and conspicuously plumose on mesepisternum, dense on upper half, scattered on lower half; scutellum with tuft of erect hairs with tips dark brown to black at each side of median line. Metapostnotum with lateral patch of short, appressed, white hairs. Propodeum with white hairs, denser along posterolateral angles. Legs with intermixed white and brown hairs; hindtibia with hairs strikingly dense on outer surface, black on basal third and white apically. Metasomal T2-T4 with broad basal bands of dense, appressed, yellowish hairs, behind such bands short, grayish hairs, posterior margins polished; T5 with grayish hairs that leave wide polished apex and longitudinal, median, polished band. *Sculpture*. Integument shiny with punctures minute, more or less dense corresponding to hairy areas; impunctate are: lower half of metepisternum, most of metapostnotum except lateral patches, propodeum below spiracle and around metapostnotum, and upper surface of T1. Metapostnotum with median basal depression and short longitudinal striae. *Morphology*. Proportion of lower to upper interocular distance 0.82-0.88:1. Head with vertex flat (fig. 29). Labrum with 3-5 small preapical denticles difficult to see due to dense pilosity; anterior margin slightly convex. Proportion of first to second flagellomere 0.86-1:1. Basal vein of forewing arising apical to vein cu-v. Proportion of lengths of submarginal cells on posterior margin 1.04-1.2:1.35-1.65. Posterior margin of first submarginal cell 1.1-1.25 times as long as apical margin. Hindtibia with stiff setae almost hidden by plumose hairs. Pygidial plate with apex narrowly rounded; in some specimens subapical spot on

disc visible, similar to that of *O. rutilans*.

*Male*. Length 5.5-8.5 mm; length of forewing 4.5-7.5 mm. Color, vestiture and punctuation similar to those of female, but scape pilose; T5 with basal band usually hidden by preceding tergum; S4 with latero-apical tuft of hairs; S5 with apical fringe of hairs. Proportion of lower to upper interocular distance 0.85-0.9:1. Proportion of first to second flagellomere 1-1.22:1. Genitalia, figures 40, 41.

*Comments*. The variation in size of this species is striking. Specimens of a series collected in the same place, the same day (Dique Cadillal, 18-XI-1983, R.B. Roberts) vary from 5.5 to 10 mm in length. This poses an interesting question about the host relations of *O. lemniscatus*. The specimens from Córdoba are paler, with the tufts on the scutellum almost completely light brown.



Figs. 40-42. *Osirinus lemniscatus*, male: 40, genitalia, dorsal and ventral; 41, genitalia, lateral; 42, sterna 7 and 8. Scale lines 0.1 mm.

*Etymology.* The specific name, beribboned in Latin, refers to the metasomal bands.

*Material studied.* Holotype female from Tafí Viejo, Prov. Tucumán, Argentina, December 1913, Curard (MACN). Following paratypes: ARGENTINA: Tucumán: 2 females, 1 male, same as holotype (MACN); 1 male, San Pedro de Colalao, Trancas, XII-1949, Foerster (SEM); 6 females, 1 male, 11 km N Dique Cadillal, 750 m, 11 and 18-XI-1983, R.B. Roberts (RBR); 1 female, Tacanas, 10-XII-1977, L. Stange (FSCA); 1 male, La Quebradita, near Tafí del Valle, 2030 m, 27-XII-1979, L. Stange (FSCA). Córdoba: 3 males, Jesus María, 14-XI-1940 (MLP).

*Osirinus rutilans* (Friese), new combination

(fig. 38)

*Osiris rutilans* Friese, 1930: 123. Type female from Bahia, Brazil (not examined). Shanks, 1986: 44-45.

I have not seen the type of *rutilans*, but its redescription by Shanks leaves no doubt about its placement in *Osirinus*. I have studied one specimen from São Paulo in the collection of the University of Kansas that Shanks attributed to *rutilans* with reservations, due to its black head and infusate wings, but that was said to be morphologically identical. The diagnostic characters used for *rutilans* in the key above are based on that specimen.

*Osirinus fritzi*, new species

(figs. 33-37)

This species is easily recognized by its integument patterned with bright reddish and black. It is allied to *rutilans*; both species share the same shape of head, the short first flagellomere, reduced vestiture and impunctate metapostnotum. *O. fritzi* is distinguished from *rutilans* by the spiculate hindtibia, the shape of the pygidial plate and the denticles of the labrum.

*Holotype female.* Length 8 mm; length of forewing 6.5 mm. Integument bright reddish with following parts black: head, antenna, lower half of pronotum, prosternum, forecoxa, mid and hindtarsi, tegula and propodeum; brownish are: mandible, foretarsus, mid and hindcoxae and trochanters, metasternum and narrow apical bands on T1-T5. Wings infusate with pterostigma and veins dark (both right wings are missing). *Vestiture* consisting of intermixed plumose and simple white hairs; hairs long and abundant around antennal sockets, side and lower third of clypeus, labrum, episterna, posterolateral angle of propodeum and legs; short, appressed on gena; rest of body with hairs sparse, scattered on polished scutum and scutellum; short and inconspicuous on discs of T2-T4. *Sculpture.* Integument shiny with minute punctures; following areas impunctate: lower half of metepisternum,

propodeum below stigma, metapostnotum, disc of T1 and apices of T2-T5. *Morphology.* Proportion of lower to upper interocular distance 0.9:1. Labrum with row of 6 small preapical denticles, the outermost smaller; anterior margin convex. Proportion of first to second flagellomere 0.6:1. Head in front view with vertex rounded (fig. 33). Basal vein of forewing meeting vein *cu-v*. Proportion of lengths of submarginal cells on posterior margin 0.9:1:1. Posterior margin of first submarginal cell 1.25 times as long as apical margin. Hindtibia along dorsal margin with stiff, basally broad and apically curved setae. Pygidial plate with apex rounded, no spot evident on disc.

*Etymology.* This species is named after Manfred Fritz, who collected the holotype, as well as so many other interesting parasitic bees.

*Material studied.* Holotype female from Palmar de Colón, Prov. Entre Ríos, Argentina (no date), M. Fritz (MACN).

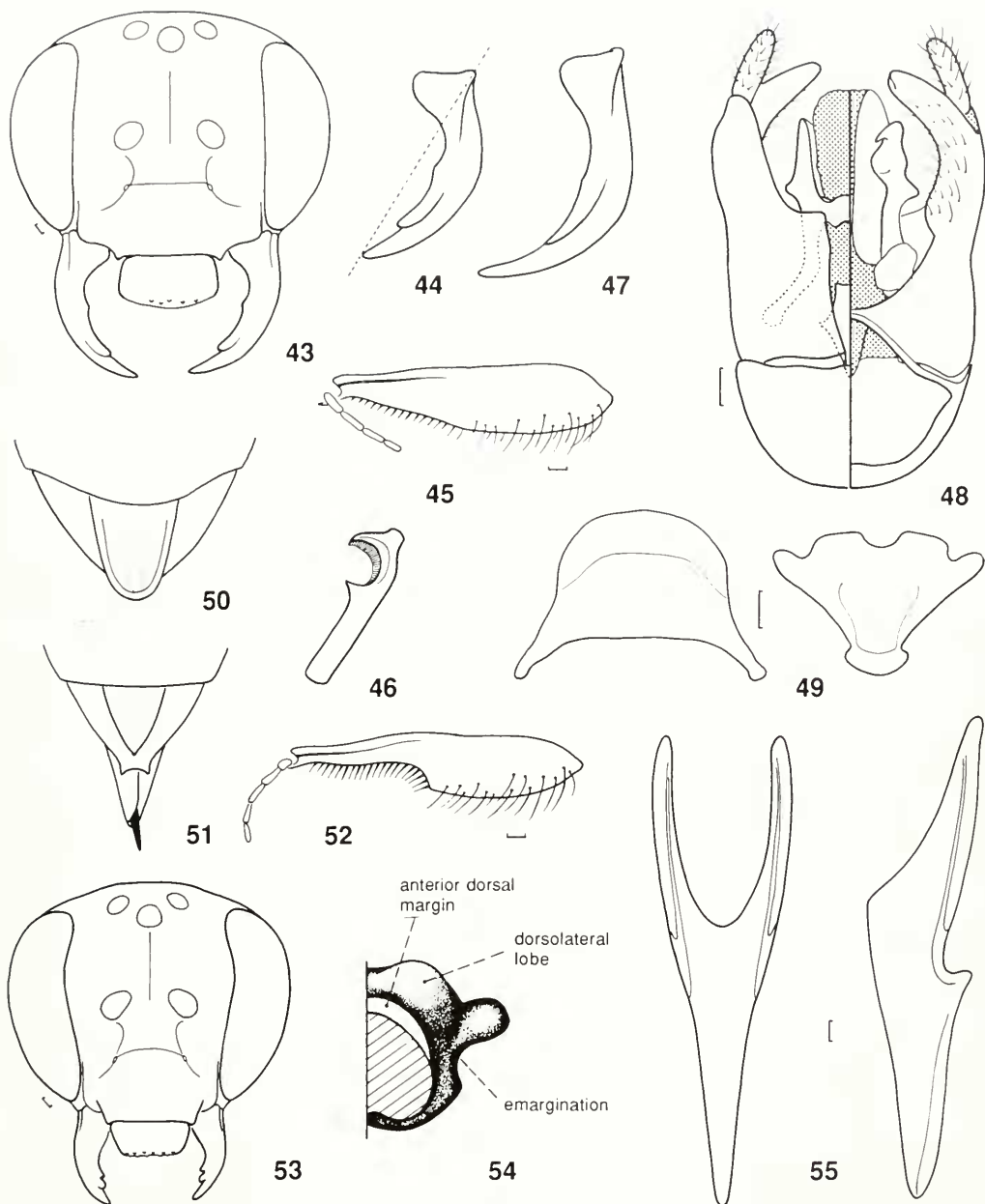
*Protosiris*, new genus

(figs 43-50)

Type species: *Osiris obtusus* Michener, 1954.

*Protosiris* recalls *Osiris* by its polished integument, the vestiture sparse, mostly simple, and the long, slender legs. It is distinguished by the integument having sparse, minute punctures; the inner margins of the eyes parallel or nearly so; the mandible long, sickle shaped, usually with one subapical tooth; and the apex of the female pygidial plate constituting the apex of the tergum. The male genitalia are as in *Osirinus*, with an articulated dorsal branch on the gonostylus.

*Description.* 1. Length 9.5-17 mm. 2. Integument dark reddish brown to entirely yellowish. 3. Integument highly polished; metapostnotum shiny, sometimes sculptured at base. 4. Vestiture short and dense on scutum; sparse, long and almost simple on rest of mesosoma, head and legs; metapostnotum always bare; metasoma with fine, short hairs to almost bare. 5. Eyes with inner margins parallel, proportion of lower to upper interocular distance 0.97-1.03:1; inner margin of eye almost straight. 6. Lateral ocellus separated from posterior margin of head by 0.7-1.2 times ocellar diameter. 7. Maximum width of gena 0.43-0.48 times maximum width of eye seen from side. 8. Preoccipital carina absent; paraocular carina short, continuing lateral margin of clypeus. 9. Malar space absent or only about 0.1 as long as width of base of mandible (*caligneus*). 10. Disc of labrum flat, with small preapical denticles. 11. Mandible long, strongly curved, with one subapical tooth or simple (*caligneus*); inner angle sometimes present. 12. Stipital comb-bearing concavity present (*mcginleyi*), or concavity reduced. 13. Maxillary palpus with 6 (*mcginleyi*) to 4 segments. 14. Hypostomal carina forming rounded angle near mandibular socket. 15. Proportion of first to second flagellomere 0.25-0.6:1. 16. Collar of pronotum with dorsolateral lobes



Figs. 43-55. *Protosiris obtusus*, female: 43, face; 44, mandible; 45, stipes; 46, forebasitarsus. *Protosiris caligneus*, female: 47, mandible. *Protosiris obtusus*, male: 48, genitalia, dorsal and ventral; 49, sterna 7 and 8. *Protosiris mcginleyi*, female: 50, T6 showing pygidial plate. *Osiris variegatus*, female: 51, apex of metasoma, dorsal aspect; 52, stipes; 53, face; 54, anterior view of pronotum, left half; 55, S6, ventral and lateral. Scale lines 0.1 mm.

globose, without median subhorizontal portion, or dorsolateral lobes flat connected by extremely short subhorizontal portion (*obtusus*). Anterior dorsal margin of pronotum not recurved; posterolateral margin not emarginate below pronotal lobe. 17. Scutum as long as intertegular span. 18. Suprateregular carina curving anteriorly close to tegula. 19. Apex of marginal cell pointed, close to wing margin. 20. Prestigma as long as wide; pterostigma 7.0-8.3 times as long as prestigma. 21. First submarginal cell with posterior margin bowed, 1.7-2.3 times as long as apical margin. 22. Basal vein of forewing arising distal to vein cu-v. 23. Jugal lobe of hind wing elongate, 0.2 as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina complete, running completely across coxa. 25. Legs slender; dorsal margin of hindtibia with stiff, basally broad and apically curved setae, intermixed with slender ones; strigular concavity of forebasitarsus 0.26-0.27 times as long as segment. 26. Metapostnotum with anterior and posterior slanting sectors, posterior one steeper. 27. Pygidial plate present in both sexes. 28. Genitalia as in *Osirinus*, but volsella present or absent.

*Comments.* The group has been treated as a species group by Shanks (1986); the reader is referred to that paper for descriptions and a key to the species. Besides *P. obtusus* (Michener) the following taxa are included: *P. caligneus* (Shanks), new combination, *P. mcginleyi* (Shanks), new combination, and *P. tricosus* (Shanks), new combination.

### Genus *Osiris* Smith

(figs. 51-55)

*Osiris* Smith, 1854: 288. Type species: *Osiris pallidus* Smith, 1854, by designation of Sandhouse, 1943: 580. Friese, 1930: 103-127. Shanks, 1986: 1-56.

*Euthygllossa* Radoszkowsky, 1884: 21. Type species: *Euthygllossa fasciata* Radoszkowsky, 1884, by monotypy.

This is the largest and most specialized of osirine genera. *Osiris* has numerous characters unique in the tribe, those shown in the cladogram and table 1 (11, 14-20) and characters 5, 8a, 9 and 14 below. The latter group of characters were

not included in the cladistic analysis because it was not possible to establish their polarity by outgroup comparison, but they also represent autapomorphies for *Osiris* in the context of the cladogram in figure 1.

Shanks (1986) redescribed the genus and presented an excellent revision of its species. The statements below are intended to complement that description with some new characters and to restrict the extent of others, due to the exclusion of several species that now belong in *Osirinus* and *Protosiris*.

*Description.* 5. Inner margin of eye with shallow emargination near upper third. 8a. Preoccipital carina present behind ocelli. 8b. Paraocular carina short, continuing lateral margin of clypeus, sometimes reaching lower third of eye (*pallidus*, *mourei*). 9. Malar space present, 0.2-0.5 times as long as basal width of mandible. 10. Labrum with row of small preapical denticles. 11. Mandible short, with two subapical teeth. 12. Stipital comb-bearing concavity present. 13. Maxillary palpus with 5 segments. 14. Hypostomal carina high, forming sharp angle near mandibular socket. 16. Pronotum with anterior dorsal margin widely recurved; posterolateral margin below pronotal lobe emarginate. 17. Scutum slightly shorter than or as long as intertegular span (0.9-1). 18. Suprateregular carina curving anteriorly close to tegula. 20. Prestigma as long as wide; pterostigma 7-8 times as long as prestigma. 21. First submarginal cell with posterior margin bowed. 22. Basal vein of forewing arising distal to vein cu-v. 23. Jugal lobe of hindwing elongate, 0.17-0.25 times as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina complete or fading near middle of coxa. 25. Hindtibia with sparse, slender hairs; strigular concavity of forebasitarsus 0.25-0.3 times as long as segment. 27. T6 of female with wide rim apical to pygidial plate; spot on plate always present, subcircular. 28. Genitalia without dorsal branch of gonostylus.

### BIBLIOGRAPHY

- Brothers, D. J. 1976. Modifications of the metapostnotum and the origin of the 'propodeal triangle' in Hymenoptera Aculeata. *Syst. Entomol.* 1:177-182.
- Ducke, A. 1907. Contribution à la connaissance de la faune hyménoptérologique du Nord-Est du Brésil. *Revue d'Entomol.* 26: 73-96.
- Ducke, A. 1908a. Zur Kenntnis der Schmarotzer Bienen Brasiliens. (Hym). *Zeitschr. Hym.* Dipt. 1908: 99-104.
- Ducke, A. 1908b. Contribution à la connaissance de la faune hyménoptérologique du Nord-Est du Brésil. II Hyménoptères récoltés dans l'Etat de Ceara en 1908. *Revue d'Entomol.* 27: 57-87.
- Ducke, A. 1910. Contribution à la connaissance de la faune hyménoptérologique du Nord-Est du Brésil. III Hyménoptères récoltés dans l'Etat de Ceara en 1909 et suppléments aux deux listes antérieures. *Revue d'Entomol.* 28: 78-109.

- Ducke, A. 1912. Die Natürlichen Bienengenera Südamerikas. Zool. Jahrb., Abt. Syst. 34(1): 51-116.
- Friese, H. 1906. Resultate einer Reise des Herrn A. C. Jensen-Haarup in die Gegend von Mendoza (Argentina). Flora og Fauna 3. Hefte: 89-102.
- Friese, H. 1908. Die Apidae (Blumenwespen) von Argentina nach der Reisergebnissen der Herren A.C. Jensen-Haarup und P. Jörgensen in den Jahren 1904-1907. Flora og Fauna 1908: 1-111.
- Friese, H. 1930. Die Schmarotzerbienengattung *Osiris* Smith (Hym.). Stett. Entomol. Zeitg. 91: 103-127.
- Giraud, J. 1863. Hyménoptères recueillis aux environs de Suse, en Piemont, et dans le département des Hautes-Alpes, en France; et description de quinze espèces nouvelles. Verh. zool.-bot. Ges. Wien 13: 11-46.
- Grütte, E. 1935. Zur Abstammung der Kuckucksbienen (Hymenopt., Apid.) Archiv. Naturg., N.F. 4 (4): 449-534.
- Jörgensen, P. 1909. Beobachtungen über Blumenbesuch, Biologie, Verbreitung usw. der Bienen von Mendoza (Hym.). Deutsch. Entomol. Zeitschr. 1909: 211-227.
- Jörgensen, P. 1912a. Revision der Apiden der Provinz Mendoza, Republica Argentina (Hym.). Zool. Jahrb., Abt. Syst. 32(2): 89-162.
- Jörgensen, P. 1912b. Los crisídidos y los himenópteros aculeados de la provincia de Mendoza. An. Mus. Nac. Buenos Aires 22: 267-338.
- Linsley, E. G. and C. D. Michener. 1939. A revision of the North American Nomadidae (Hymenoptera). Trans. Am. Entomol. Soc. 65: 265-305.
- Michener, C. D. 1944. Comparative external morphology, phylogeny and a classification of the bees. Bull. Amer. Mus. Nat. Hist. 82: 151-326.
- Michener, C. D. 1954. Bees of Panamá. Bull. Am. Mus. Nat. Hist. 104: 1-176.
- Michener, C. D. 1965. A classification of the bees of the Australian and South Pacific Regions. Bull. Am. Mus. Nat. Hist. 130: 1-362, 15 pl.
- Michener, C. D. 1986. Family group names among bees. Jour. Kansas Entomol. Soc. 59: 219-234.
- Michener, C. D. and A. Fraser. 1978. A comparative anatomical study of mandibular structure in bees. Univ. Kansas Sci. Bull. 51(14): 463-482.
- Michener, C. D. and L. Greenberg. 1980. Ctenoplectridae and the origin of long-tongued bees. Zool. J. Linn. Soc. 69: 183-203.
- Michener, C. D. and J. S. Moure. 1957. A study of the classification of the more primitive non-parasitic anthophorini bees (Hymenoptera, Apoidea). Bull. Am. Mus. Nat. Hist. 112: 399-451.
- Popov, V. V. 1939. Relationships of the genus *Osiris* F. Smith and its position in the system of bees (Hymenoptera, Apoidea). Comptes Rendus Acad. Sci. de l'URSS 25(2): 163-166.
- Popov, V. V. 1958. Peculiar features of correlated evolution of two genera of bees—*Macropis* and *Epeoloides* (Hymenoptera, Apoidea)—and a plant genus *Lysimachia* (Primulaceae). Revue d'Entomol. URSS 37(3): 499-519. (in Russian)
- Radoszkowsky, O. 1884. Quelques nouveaux Hyménoptères d'Amérique. Horae Societatis Entomol. Rossicae 18: 17-22.
- Rozen, J. G., Jr. 1966. The larvae of the Anthophoridae (Hymenoptera, Apoidea). Part 2. The Nomadinae. Am. Mus. Novitates 2244: 1-38.
- Rozen, J. G. Jr. 1984. Comparative nesting biology of the bee tribe Exomalopsini (Apoidea, Anthophoridae). Am. Mus. Novitates 2798: 1-37.
- Rozen, J. G. Jr., K. R. Eickwort and G. C. Eickwort. 1978. The bionomics and immature stages of the cleptoparasitic bee genus *Protepeolus*. Am. Mus. Novitates 2640: 1-24.
- Ruiz, F. 1935. Algunas notas entomológicas. Rev. Chilena Hist. Nat. 39: 271-278.
- Sandhouse, G. A. 1943. The type species of the genera and subgenera of bees. Proc. U.S. Nat. Mus. 92: 519-619.
- Shanks, S. S. 1986. A revision of the neotropical bee genus *Osiris* (Hymenoptera: Anthophoridae). The Wasmann Jour. Biol. 44(1-2): 1-56.
- Smith, F. 1854. Catalogue of hymenopterous insects in the collection of the British Museum. Part II Apidae. London. pp. 199-465, pls. 7-12.
- Snelling, R. R. 1984. Studies on the taxonomy and distribution of American centridine bees (Hymenoptera: Anthophoridae). Contributions in Science, Los Angeles Co. Museum 347: 1-69.
- Swenk, M. H. 1907. The bees of Nebraska.-III. Entomol. News 18(7): 293-300.
- Warncke, K. 1982. Zur Systematik der Bienen - Die Unterfamilie Nomadinae (Hymenoptera, Apidae). Entomofauna 3(8): 97-128.
- Winston, M. L. 1979. The proboscis of the long-tongued bees: a comparative study. Univ. Kansas Sci. Bull. 51(22): 631-667.